BOOK REVIEW

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The Development and Evolution of Butterfly Wing Patterns.—H. F. Nijhout. 1991. Smithsonian Institution Press, Washington and London. 297 pp. $20 paper, $45 cloth.

The variety of bright colors and intricate patterns on butterfly wings has probably kindled more careers in entomology and evolutionary biology than any other attribute of insect morphology. The vast numbers of butterflies in insect collections, the existence of commercial butterfly houses, and the drive to make a butterfly our national insect, all attest to butterflies' immense popularity. But, in addition to serving as the public relations poster children for the study of insects, the Papilionoidea have been of fundamental importance to biological research throughout history. Butterflies were influential to Darwin, Wallace, and Fisher in formulating their selection theories. More recently, research on butterflies has provided paradigms for such diverse fields as chemical ecology, coevolution, and Pleistocene refugium biogeography. A prescient H. W. Bates forecast in 1864 (as Nijhout quotes in his preface) that "the study of butterflies . . . will some day be valued as one of the most important branches of biological science."

Ironically, one area of butterfly biology that has received surprisingly little attention over the years is the evolution of the very wing patterns that attract so many people to study butterflies in the first place. In spite of the zealous naming of innumerable subspecies, races, variations, hybrids and aberrations on the basis of wing pattern variation, few synthetic studies of pattern evolution have been carried out. Those that exist have sunk into premature and undeserved obscurity. This book endeavors to reestablish the study of butterfly wings as a paradigm for evolutionary and developmental research.

In *The Development and Evolution of Butterfly Wing Patterns,* Nijhout resurrects classic studies by Schwanwitsch and Süffert from the 1920's, and synthesizes them with his own results into a relatively simple, comprehensive model of wing pattern development. The central premise of this model is that a homologous, ancestral pattern exists, the "nymphalid groundplan," from which the patterns of all nymphalids, and perhaps even of all Lepidoptera, can be derived. Nijhout presents his case clearly and thoroughly, building up from empirical results and the historical models to his own elaborate mechanistic hypothesis of wing pattern development. It is obviously essential to provide illustrations in a book about pattern evolution, and Nijhout succeeds admirably here. The book is profusely illustrated with figures reproduced from prior works, new half-tone photos and line drawings, and eight attractive color plates.

The first six chapters provide background and attempt to establish the orthodoxy of the wing-pattern developmental process. Chapter One introduces wing and scale morphological development, basic pigment chemistry and the critical idea of the wing as a static cellular monolayer. Chapters 2–4 lay out the Schwanwitsch-Süffert nymphalid groundplan concept and explore its themes and variations across a variety of intuitively problematical taxa, including the leaf butterfly, *Kallima inachus* (Nym-

phalidae: Nymphalinae), *Charaxes* (Nymphalidae: Charaxinae) and *Heliconius* (Nymphalidae: Heliconiinae). Nijhout argues that essentially any wing pattern can be homologized to the hypothetical groundplan, and further that serial pattern homology exists at several levels among wing cells and between fore and hindwings. Chapter Five presents experimental results which show that radical and complex changes in adult morphology can be produced by simple manipulations at precise developmental stages. Polymorphism, mimicry and polyphenism are discussed at length in Chapter Six, apparently to the end of demonstrating how these phenomena do not violate the general model, contrary to appearances. I suspect that most readers will find the 20-page explication of *Heliconius* wing-pattern genetics to be somewhat overwhelming.

The core of this book, Nijhout's model for pattern generation during development, is presented in Chapter Seven. The basic idea is that a set of static sources for a pattern-inducing signal are distributed in fixed positions across the wings. These points release the signal substance by diffusion at particular times during development. Patterns can evolve by the repositioning of these sources, and by shifts in timing or amount of signal production from a given source. Chapter Eight explores implications of the model, and suggests hypotheses for future research. An unexpected and valuable bonus to the book is the inclusion of two systematic appendices. The first presents recent phylogenies for major butterfly groups drawn from the literature, while the second is an important new cladistic classification of nymphalid subfamilies, tribes and genera by D. J. Harvey.

Nijhout presents his model of butterfly wing pattern evolution elegantly, carefully, and without any major flaws that I could detect. It is, in fact, difficult to envision any hypothetical wing pattern that could not be explained by his scheme. This is a mixed blessing, of sorts, because it reduces our interest in wing patterns as historical phenomena useful for systematics: all patterns become developmental homologs of one another and thus all apparent synapomorphies can be equally well-explained as parallelisms. The model implies that differences in wing patterns among taxa must be viewed as the phenotypic manifestation of recent selective forces for mimicry, sexual selection, crypsis, aposematism or other unidentified phenomena. On the other hand, the model also suggests that the genetic control of pattern formation is reasonably simple, depending more on differential local regulation of simple pattern-inducing substances than on complex arrays of pattern-producing "supergenes." If this is true, then perhaps some of Nijhout's hypotheses may soon be accessible to testing with molecular techniques, providing potentially enormous insights into the genotype-phenotype black box.

Although this book is fairly technical, and neither a desk reference nor a bedtime page-turner for the casual butterfly enthusiast, I found it to provide a novel, thought-provoking approach to the classic evolutionary problem of the development of complex features. In many respects, the book would be more sensibly shelved by subject, with other books on development, than by taxon, in the Lepidoptera section. The two-dimensional, static arrangement of cells in butterfly wings is a simple and tractable template for both theoretical and experimental manipulation in the study of development (reconfirming Bates' assertion that butterflies will become ever more important as model organisms across all branches of biology). That the resulting patterns also happen to be beautiful is serendipitous.—*Andrew V. Z. Brower, Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853.*